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Biogeomorphologic succession (i.e. reciprocal adjustments between vegetation and geomorphologic dynamics) of the Mediterranean River Tech, France, was analysed using aerial photographs over a period of sixty years between 1942 and 2000. A spatial analysis of the biogeomorphologic succession was undertaken considering effects of flood regime. Interactions between vegetation dynamics and flood events largely controlled the spontaneous replacement of the dense riparian forest removed in October 1940 during an exceptional high magnitude flood event with a recurrence time >100 yr. In response to this major disturbance event, the fluvial landscape demonstrated a very high resilience emphasizing the existence of a positive feedback driven by pioneer riparian vegetation. The observed feedback corresponded to landform accretion, vegetation succession and to an increase of biogeomorphologic stability under current hydrogeomorphologic and bioclimatic conditions. The evolution of the biogeomorphologic system toward stabilisation appeared to be non-linear with a threshold occurring thirty years after the exceptional destructive flood event. This threshold materialized a reinforcement of biogeomorphologic cohesive forces driven by vegetation dynamics. This study showed the control of riparian vegetation on the dynamics of Mediterranean fluvial landscapes and pointed to the need to improve our knowledge about biogeomorphologic succession cycles and threshold dynamics within different biogeomorphologic settings.

Riparian vegetation dynamics depend on hydrogeomorphologic parameters (Stromberg et al. 1991, Florsheim et al. 2008), and in return living and dead riparian plants modulate sediment, diaspore, nutrient and water flows within fluvial corridors (Gurnell et al. 2005, Opperman et al. 2008). Fluvial corridors are constituted of river channels, their margins and the zone of expansion of frequent floods occupied by riparian vegetation. Under intermediate and highly dynamic settings, negative and positive feedbacks between water, sediment and vegetation dynamics produce a complex and shifting mosaic of habitats, landforms and associated vegetation communities (Ward et al. 2002, Steiger et al. 2005). Biogeomorphologic positive feedbacks occur where plant growth or reproduction is controlled by hydrogeomorphologic processes; and where these hydrogeomorphologic processes are to some extent regulated by the characteristics of vegetation (Francis et al. 2009). The ability of some riparian plants to grow on deposited sediment implies that sediment deposition favours plant biomass production. In return, biomass production then increases surface roughness and sediment deposition (Francis 2006, Corenblit et al. 2009a). An increasing body of research demonstrated over the last thirty years the control of dead or living vegetation on hydrodynamics (Green 2005), fluvial morphogenesis (Hupp and Osterkamp 1996) and fluvial landscape dynamics (Ward et al. 2002, Pettit and Naiman 2005). These studies suggested that vegetation plays key roles in determining fluvial ecosystem structure, function and channel geometry. However, only recent investigations focused explicitly on feedbacks between hydrogeomorphologic and riparian vegetation dynamics (Bendix and Hupp 2000, Naiman et al. 2000, Dollar et al. 2007). In particular, the fundamental role of pioneer vegetation and dead wood in creating, maintaining and constructing fluvial landscapes in early stages of succession has been illustrated only recently (Johnson 1994, Gurnell et al. 2001, 2005, Naiman et al. 2005). The resulting effects on fluvial ecosystem structure and function have been demonstrated at local scales from single plants to community patches, and pioneer riparian vegetation including herbs, shrubs and young trees have now explicitly been identified in fluvial systems as "ecosystem engineers" sensu Jones et al. (1994) (Edwards et al. 1999, Gurnell and Petts 2006, Corenblit et al. 2008, Francis et al. 2009).

The synergic development of fluvial landforms and vegetation communities (i.e. biogeomorphologic succession) driven by pioneer engineering riparian vegetation corresponds to a positive feedback materialized by the shift from a strictly hydrogeomorphologically driven system dominated by bare sediment to an autogenic ecologically driven system dominated by stabilized, forested, and only periodically flooded riparian islands and floodplains (Gurnell et al. 2001, Geerling et al. 2006, Corenblit et al. 2007, Francis et al. 2009). The biogeomorphologic succession is composed of four main phases during which particular sets of biophysical processes take place (for a full description see Corenblit et al. 2007): 1) geomorphologic, i.e. bare sediment, during alluvial bar accretion or after vegetation destruction by floods; 2) pioneer, i.e. seedling and saplings on the bare or rejuvenated alluvial bars; 3) biogeomorphologic, i.e. pioneer herbs, shrubs or trees on the alluvial bars within the exposed zones of the active channel; and 4) ecological, i.e. riparian forests on stabilized and disconnected islands and floodplains. Pioneer riparian vegetation plays its crucial engineering role (sensu Jones et al. 1994) by trapping sediment and preventing erosion mainly during the biogeomorphologic phase which is characterised by a high degree of hydrogeomorphologic connectivity.

In the current European and North American bioclimatic settings, the cycle of biogeomorphologic succession (i.e. from rejuvenated stages materialised by the domination of bare substrates to mature stages characterized by the domination of dense post-pioneer riparian forests which may in turn be rejuvenated, starting the cycle over again) alternates between periods of biogeomorphologic organisation toward mature and stabilized stages, and sudden and brief periods of succession rejuvenation which coincide with exceptional floods (Décamps et al. 1988, Hughes 1997, Gurnell et al. 2001). The balance between resistive forces largely controlled by vegetation and destructive or regenerative forces determined by the hydrogeomorphologic disturbance regime is critical in defining the frequency and the spatial extent of biogeomorphologic regression or progression in succession (Baptist et al. 2004).

The biogeomorphologic succession dynamics were studied in this article at the reach scale specifically in a Mediterranean context within the fluvial corridor of the River Tech, over a period of sixty years from 1942 to 2000. Two main questions were addressed using the River Tech as a case study. 1) Within a Mediterranean context, contrasted in respect to flow regime, does pioneer riparian vegetation generate positive feedbacks leading to vegetation succession combined with floodplain construction and stabilisation? If the response is positive, over which time spans act these positive feedback mechanisms? 2) Is the biogeomorphologic succession in the Mediterranean context linear in time and homogenous in space? A biogeomorphologic succession would be considered being homogenous in space when the quality (vegetation physiognomy) and the time required in reaching post-pioneer stages are identical in each location. In order to answer these questions, the spatial and temporal dynamics of biogeomorphologic succession of the River Tech were quantified and simulated using respectively geographical information systems (GIS) and the Markov chain.

Material and methods

Study reach

The River Tech, western Pyrenees, France, is a 85 km long gravel bed river which drains a Mediterranean mountainous catchment of 750 km^2 (Fig. 1). The contrasted pluvio-nival hydrological regime reflects the Mediterranean influence, with high flows occurring from April to May and from November to January (10–13 $m^3 s^{-1}$), and low flows occurring between July and September (4–5 $m^3 s^{-1}$). High magnitude flash floods generally occur in autumn when riparian vegetation is fully developed. This river was chosen because it remains a relatively natural system compared to most French and European rivers. Furthermore, a very exceptional and destructive flood with a peak discharge of 2500 $m^3 s^{-1}$ recorded in the piedmont zone occurred in October 1940. Before this destructive flood, the River Tech was occupied by dense riparian forests (Jacob 1995). Aerial photographs document that erosion during the 1940 flood completely removed riparian vegetation within the entire fluvial corridor. The present study uses this context of a completely rejuvenated river system with only bare sediment within the entire fluvial corridor as its reference situation for the analysis of biogeomorphologic succession dynamics.

Hydrogeomorphologic dynamics

The flood regime, i.e. the magnitude, frequency, duration, and timing of floods, is a main control of fluvial landscape dynamics (Poff et al. 1997, Naiman et al. 2008). A hydrological time series established from peak discharges ≥ 300 $m^3 s^{-1}$ (return period = 1 yr) recorded since 1940 at a gauging station 2 km upstream from the study reach, was used to characterize the flood regime of the River Tech during the five different periods determined according to the dates of the aerial photographs (1942–1953, 1953–1962, 1962–1974, 1974–1988, and 1988–2000). Change analyses of river planform geometry were performed in order to quantify geomorphologic changes associated with the flood disturbance regime for each of the five periods. Measurements using the GIS MapInfo™ included four variables: 1) active channel area (m^2). The active channel on aerial photographs corresponded to water channel plus bare sediment. It is the most exposed and unstable zone within the fluvial corridor (Gurnell et al. 2005); 2) mean active channel width (m) measured with MapInfo™ every 100 m along the main channel, with a total of 52 transects; 3) lateral mobility of the main channels between two successive dates. The distance (m) measured between the main active channels at time $t-1$ and time t on the 52 transects was used to represent mobility; 4) sinuosity index (Schumm 1963) or braiding index (Brice 1960) according to whether the river pattern was meandering or braiding. The sinuosity presents a measure of the intensity of channel meandering and the braiding index a measure of the overall braiding

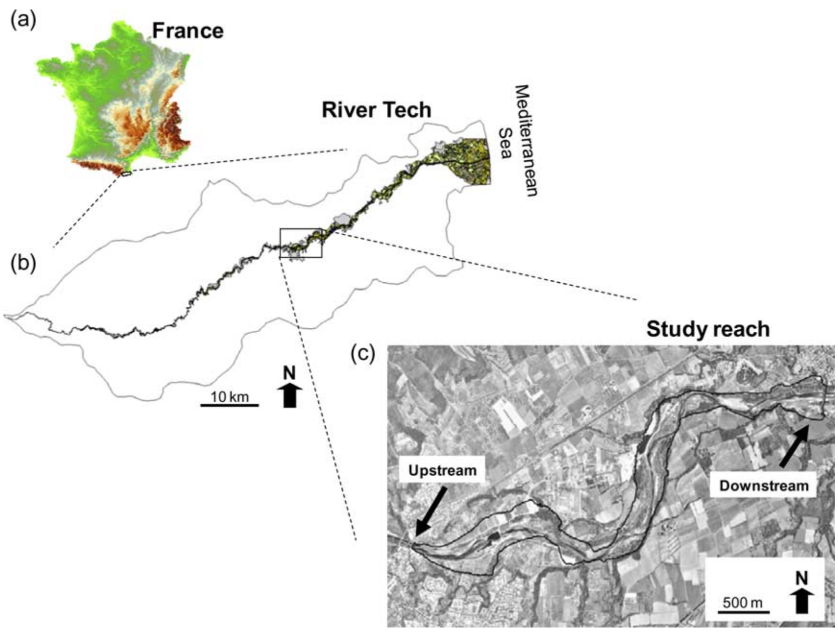

Figure 1. Study reach location. Upstream limit: 42°29′N, 2°44′E, altitude 103 m a.s.l.; downstream limit: 42°30′N, 2°47′E, altitude 90 m a.s.l. The River Tech catchment (b) is located in the SE of France (a). The active channel and its floodplain are represented in (c). The flow direction is from W (source) to E (Mediterranean Sea).

intensity of the river. The statistical significance of differences between dates was tested using one-way analyses of variance (ANOVA). ANOVAs were performed with repetition because spatial measurements were repeated in the same location at different dates and thus the data did not follow the criterion of independence.

Biogeomorphologic succession dynamics

The diachronic study of the biogeomorphologic succession dynamics of the River Tech was carried out using GIS-based analysis (MapInfo™). The spatial analyses were undertaken within a 5 km long river reach selected in the piedmont zone of the River Tech (Fig. 1). They were based on six sets of black and white aerial photographs with scales ranging from 1:17 000 to 1:30 000 and covering a period of sixty years: 1942, 1953, 1962, 1974, 1988 and 2000. The choice of biogeomorphologic succession analyses at ten year periods was validated by testing shorter, three year periods, of two complementary black and white aerial photograph sets taken in between each of the ten year period. This qualitative control of landscape structural change based on stereoscopic analyses attested the continuity in changes between dates used for measurements at the step of ten years. All aerial photographs were taken during the vegetation growth period in July and August. Daily discharges during these different low water periods were equivalent between all dates ($\sim 5\ m^3\ s^{-1}$). Aerial photographs were georeferenced with MapInfo™. Quadratic error was estimated as <5 m. The spatial extent of the study area and its lateral limits, corresponding to the topographic break line of the Holocene terraces, were defined from the 1942 aerial photographs and during field investigations.

Four phases based on the biogeomorphologic succession classification established by Corenblit et al. (2007) were defined on aerial photographs using MapInfo™: 1) geomorphologic/pioneer dominated by bare sediment; 2) biogeomorphologic dominated by dense herbs; 3) biogeomorphologic dominated by sparse or dense shrubs; 4) ecological dominated by dense trees. Areas dominated by human activities were also digitized. A regular grid of 10×10 m, constituting 19 000 georeferenced squares of $100\ m^2$, represented the basic framework for the spatial analysis based on the distance measured between the main active river channels at all different dates.

The biogeomorphologic succession dynamics were analyzed for each period by calculating surface cover of each of the four biogeomorphologic succession phases. Three different diversity indexes were calculated to define related landscape properties: Shannon Diversity (H′), dominance (D) (for explanations and formulas see Hammer et al. 2001), and fragmentation which is the number of disjointed objects of a same thematic category (Bogaert et al. 2000). In order to quantify the transition dynamics between biogeomorphologic succession phases, and to estimate the absorbing or attractive power of the mature ecological phase, the transitions were calculated for each period of time between successive aerial photographs. This work was performed through transition analyses using transition matrix established from the GIS-approach. The matrix describes the dynamics of the system between two dates where each element of the matrix represents the individual transition probability calculated for one biogeomorphologic phase shifting to another biogeomorphologic phase after one time increment. Transition analysis was performed 1) at the reach scale in order to define the general tendencies of biogeomorphologic succession between 1942 and 2000; and 2) along the transverse gradient of hydrogeomorphologic disturbance from the main channels to the floodplain, in order to perform a spatial analysis of the biogeomorphologic succession. The distance (m) to the main active channels from their position at time $t-1$ was used in order to analyze the combined effect of the initial state within each 10×10 m grid cell and their location along the transverse disturbance gradient.

A Markov chain (Markov 1907, Usher 1981, Turner 1987, Balzter 2000, Coppedge et al. 2007) was applied at the reach scale in order to simulate and quantify the frequency and the mean return and maintenance times of each phase of the biogeomorphologic succession and for each couple of dates. The Markov chain was parameterised by the transition probabilities between the discrete states of the biogeomorphologic succession. The probability distributions were defined using the GIS transition matrix for each couple of dates (Supplementary material Table S1).

Biogeomorphologic succession maturation (progression in succession, i.e. from phase 1 to 4) versus rejuvenation (regression in succession, i.e. from phase 4 to 1) dynamics were studied on the transverse gradient within the fluvial corridor. In order to perform this analysis four different transition classes of maturation and five transition classes of rejuvenation were defined (Fig. 2). All statistical analyses were performed with SYSTAT v. 11 and PAST v. 1.27 (Hammer et al. 2001).

Results

Hydrogeomorphologic dynamics

The flood regime of the River Tech showed highly irregular and contrasted dynamics (Table 1). The associated geomorphologic responses were also contrasted with a highly dynamic period in the 1960s and 1970s and a loss of dynamics after this period (Table 2). The simple linear regression models showed that the variables of control for geomorphologic changes were mainly 1) the flood peak discharge ($n = 6$ for each model): channel mobility: $F = 41.07$, $p < 0.01$, $R^2 = 0.91$; active channel surface area: $F = 26.27$, $p < 0.01$, $R^2 = 0.87$; active channel mean width: $F = 28.90$, $p < 0.01$, $R^2 = 0.88$ and 2) the average flood peak discharges ($n = 6$ for each linear regression models): channel mobility: $F = 57.77$, $p < 0.01$, $R^2 = 0.93$; active channel surface area: $F = 21.09$, $p = 0.01$, $R^2 = 0.84$; mean active channel width, $F = 19.90$, $p = 0.011$, $R^2 = 0.83$. One way ANOVAs showed the statistical significance of the adjustments between the different periods for the mean

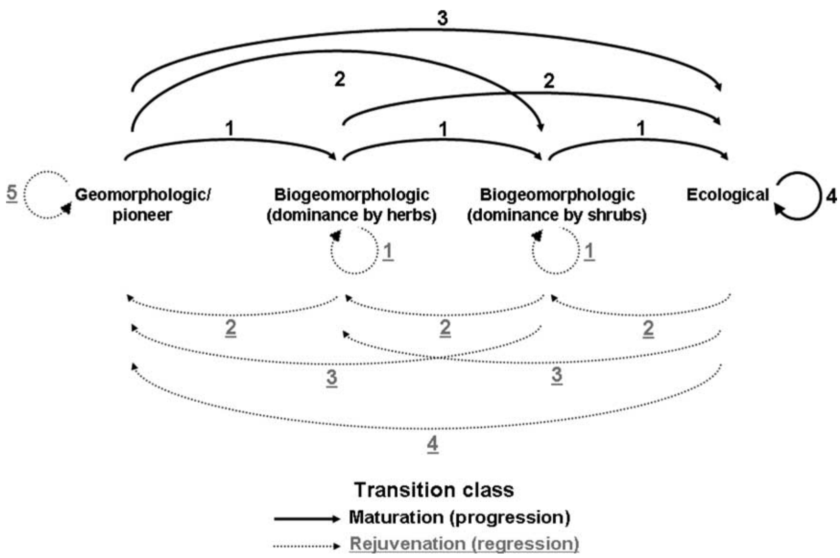

Figure 2. Model showing the different possibilities of maturation and rejuvenation processes observed on the River Tech, defined here as transition classes between the four phases of biogeomorphologic succession (geomorphologic/pioneer phase; biogeomorphologic phase (dominance by herbs); biogeomorphologic phase (dominance by shrubs); ecological phase). The processes of maturation (plain arrows) present four transition classes: 1) progressive changes from one biogeomorphologic succession phase to the next (e.g. from geomorphologic/pioneer to biogeomorphologic dominated by herbs); 2) changes from one biogeomorphologic succession phase to the second next one (e.g. from the geomorphologic/pioneer phase directly to biogeomorphologic dominated by shrubs without the establishment of the biogeomorphologic phase dominated by herbs); 3) changes from the first to the last biogeomorphologic succession phase (from the geomorphologic/pioneer phase directly to the ecological phase without the establishment of the biogeomorphologic phase dominated by herbs nor the biogeomorphologic phase dominated by shrubs); 4) no changes. The processes of rejuvenation (dotted arrows) present five transition classes: 1) no changes; 2) regressive changes from one successive phase to the next (e.g. from ecological to geomorphologic/pioneer); 3) regressive changes from one successive phase to the second next one (e.g. from ecological directly to biogeomorphologic dominated by herbs without the establishment of the biogeomorphologic phase dominated by shrubs); 4) regressive changes from the last to the first biogeomorphologic succession phase, i.e. from the ecological phase directly to the geomorphologic phase without the establishment of the biogeomorphologic phase dominated by shrubs or by herbs; 5) no changes; i.e. persistence in the geomorphologic/pioneer phase.

Table 1. Characterization of the flood regime for each time period investigated. Standard deviation is indicated for the average of flood peak discharges. The flood regime was highly contrasted between 1940 and 2000: a single catastrophic flood between 1940 and 1942; no floods between 1942 and 1953; a resumption of several intermediate to high magnitude floods between 1953 and 1962; a succession of high magnitude floods between 1962 and 1974; and high magnitude floods remaining frequent between two periods, 1974–1988 and 1988–2000.

Period	Average of flood peak discharges ($m^3\ s^{-1}$)	Flood peak discharge ($m^3\ s^{-1}$)	Number of floods $>300\ m^3\ s^{-1}$
1940–1942	2500 ± 0	2500	1
1942–1953	500 ± 0	500	1
1953–1962	618 ± 266	1000	5
1962–1974	727 ± 331	1400	14
1974–1988	724 ± 280	1130	7
1988–2000	761 ± 299	1200	7

active channel width: $F_{4,255} = 25.6$, $p < 0.0001$; and for channel mobility: $F_{5,306} = 145$, $p < 0.0001$.

Biogeomorphologic maturation versus rejuvenation along the transverse gradient of disturbance

Spatial analysis of biogeomorphologic maturation versus rejuvenation along the transverse gradient of disturbance revealed a tendency to maturation toward biogeomorphologic stability materialised by the dominance of the ecological phase (phase 4 of the biogeomorphic succession) and the decrease in landscape diversity (Table 3). Biogeomorphologic maturation corresponded to the progressive colonization of the floodplain by dense riparian forests which started initially between 1942 and 1953 within the immediate margin of the active channels.

The zones adjacent to the initial (1942) position of the active channels evolved between the first ten year period between 1942 and 1953 without floods (Table 1) mainly toward the ecological phase, whilst the more distant zones developed toward the biogeomorphologic phase with sparse pioneer herbaceous and shrubby covers (Fig. 3 and 4; Table 3). Figure 5 illustrates the clear establishment of these two contrasted succession patterns.

The biogeomorphologic succession was completely rejuvenated according to the resumption of floods between 1953 and 1974 mainly in the first 30 m of the active channels (Fig. 3 and 4; Table 3). Conjointly, a large proportion (around 50%) of the sparse herbaceous and shrubby communities observed in 1953 beyond the first 30 m from the active channels were not removed by water flow and evolved toward the ecological phase with dense riparian forests. The transition analysis (Supplementary material Table S1) clearly revealed that the probability of rejuvenation decreased systematically as a function of the initial maturation phase of the biogeomorphologic succession (i.e. low probability of rejuvenation from previous biogeomorphologic and ecological phases) and the distance to main active channels (Fig. 6).

After a period of thirty years a so far unequivocal maturation in succession from the outer limits of the fluvial corridor to the margins of the active channels occurred. The maturation transition class number 4 (see Fig. 2 for explanation) described in Fig. 3 and 4 occurred systematically beyond 170 m from the active channels after 1974. The occurrence of the maturation transition class number 3 implicating a direct evolution from bare substrate (geomorphologic/pioneer phase) to dense riparian trees (ecological phase) (Fig. 2) was particularly stimulated according to the proximity of active channels (Fig. 3 and 4). Complete rejuvenation, i.e. the creation or maintenance of bare sediment, tended to concentrate during the last twenty years only within the first ten meters at the proximity of active channels (Fig. 3 and 4) despite the occurrence of several intermediate to high magnitude floods (Table 1).

Markov chain

The Markovian analysis with an iteration step of ten years (1000 iterations) based on the previous calculated transition matrix for each couple of dates showed the low frequency of occurrence of the biogeomorphologic phase for each period between 1942 and 2000 (Fig. 7; Table 4). The biogeomorphologic phase appeared to be unstable and transitory. Conversely, the frequency of occurrence of the ecological phase was high. From a given date to the next, the biogeomorphologic phase showed systematically a tendency to progress toward the ecological phase (Fig. 6). The Markovian simulation, based on the transition matrix calculated for the period without floods (1942–1953), revealed a clear tendency toward stabilization of the landscape structure; the biogeomorphologic succession was achieved over a thirty year period simulated at the scale of the corridor with 100% of domination by the ecological phase (Fig. 7; Table 4). This Markov chain can be

Table 2. Evolution of the planform geometry of the River Tech determined from the quantification of different geomorphologic variables. Standard deviations are indicated for the channel mobility and the active channel mean width.

Geomorphologic variable	1940–1942	1942–1953	1953–1962	1962–1974	1974–1988	1988–2000
Channel mobility (m)	255 ± 0	7 ± 10	27 ± 39	90 ± 79	35 ± 42	21 ± 26
Active channel surface area (m^2)	1 007 510	73 761	412 029	448 399	235 791	153 045
Active channel mean width (m)	225 ± 83	15 ± 7	87 ± 35	107 ± 56	51 ± 26	34 ± 18
Braiding index (Brice 1960)	2.78	1.51	2.40	2.43	1.97	1.45
Sinuosity index (Schumm 1963)	1.36	1.33	1.25	1.24	1.22	1.23

Table 3. Biogeomorphologic succession dynamics and resulting fluvial landscape diversity. GEO/PION = geomorphologic/pioneer phase; BIOGEO_HERB = biogeomorphologic phase with herbs; BIOGEO_SHRU = biogeomorphologic phase with shrubs; ECOL = ecological phase; HA = human activity.

	1942	1953	1962	1974	1988	2000
Total surface (m^2)						
GEO/PION	1 007 510	73 761	412 029	447 711	235 790	153 045
BIOGEO_HERB	86 771	285 000	571 106	38 378	169 46	15 015
BIOGEO_SHRU	168 483	235 039	193 038	183 036	137 241	199 684
ECOL	0.00	468 073	415 569	396 377	376 273	483 212
HA	0.00	118 215	114 190	182 543	491 253	375 009
Relative cover (%) with HA						
GEO/PION	79.79	6.25	34.57	35.87	18.75	12.48
BIOGEO_HERB	6.87	24.15	4.79	3.08	1.35	1.22
BIOGEO_SHRU	13.34	19.92	16.19	14.67	10.91	16.29
ECOL	0.00	39.66	34.87	31.76	29.92	39.41
HA	0.00	10.02	9.58	14.63	39.07	30.59
Relative cover (%) without HA						
GEO/PION	79.79	6.95	38.23	42.02	30.77	17.99
BIOGEO_HERB	6.87	26.84	5.30	3.60	2.21	1.76
BIOGEO_SHRU	13.34	22.14	17.91	17.17	17.91	23.47
ECOL	0.00	44.08	38.56	37.20	49.11	56.78
Landscape diversity with HA						
Shannon (H′)	0.56	1.79	1.92	2.01	2.20	2.05
Dominance (D)	0.70	0.23	0.22	0.19	0.15	0.21
Landscape diversity without HA						
Shannon (H′)	0.56	1.05	1.35	1.33	1.24	1.15
Dominance (D)	0.70	0.48	0.33	0.33	0.41	0.47
Number of patches						
GEO/PION	119	14	151	142	142	83
BIOGEO_HERB	127	178	86	70	33	22
BIOGEO_SHRU	344	438	473	503	367	273
ECOL	0.00	54	78	63	65	77
HA	0.00	72	62	93	182	149
Total	590	756	850	871	789	604

characterized as "absorbent" because the ecological phase represented a unique attractor state. The periods marked by floods (1953–1962, 1962–1974, 1974–1988, and 1988–2000) oscillated mainly between the geomorphologic/pioneer phase and the ecological phase with a rapid transition of less than ten years through the biogeomorphologic phase (Fig. 7; Table 4). The Markovian analysis also demonstrated the general tendency of the fluvial corridor 1) to a progressive decrease of the occurrence frequency of the geomorphologic/pioneer phase and 2) to a net increase in frequency of the ecological phase which appeared to be more and more absorbent in time at the scale of the corridor (Table 4). Considering the biogeomorphologic succession, the absorbance efficiency of the ecological phase reached its maximum at the scale of the fluvial corridor after thirty years. The colonization by dense riparian forests of the areas distant from the active channels ultimately stimulated vegetation growth and succession close to the active channels. In accordance with these landscape dynamics, the transitory biogeomorphologic phase at a short timescale (ten year resolution) was difficult to observe by the simulations.

Discussion

Feedback dynamics

This study illustrated the role of riparian vegetation dynamics in structuring fluvial landscapes in space and time at the reach scale. In the Mediterranean context of the River Tech the interactions between riparian vegetation and hydrogeomorphologic disturbances clearly generated a positive feedback that rippled through the entire fluvial corridor in thirty years following the flood of October 1940 which entirely destructed and cleared the riparian forest. This time period corresponds to the relaxation time of the River Tech fluvial landscape structure. Such resilience dynamics of construction and stabilization of islands and floodplains with riparian forests within a few decades were observed in the temperate context on the River Tagliamento, Italy (Edwards et al. 1999, Gurnell et al. 2001, Gurnell and Petts 2006), on many other French rivers (Pautou et al. 1997, Piégay and Salvador 1997, Liébault and Piégay 2002), and in North America (Miller et al. 1995, Friedman et al. 1996). Similar positive feedbacks between hydrogeomorphologic processes and vegetation dynamics were also described in tropical rivers where riparian vegetation contributes to concentrate matter and energy flows within active channels constrained by dense riparian forests (Junk and Furch 1993, Wende and Nanson 1998). It is suggested that these positive feedback dynamics occur in temperate, and also in tropical contexts mainly because 1) vegetation growth and resilience are regularly stimulated by the climatic conditions within these regions; and because 2) flood regimes encompass high frequency and low to intermediate magnitude events which contribute to support the continuity of the process of landform construction by delivering fine sediment between destructive floods

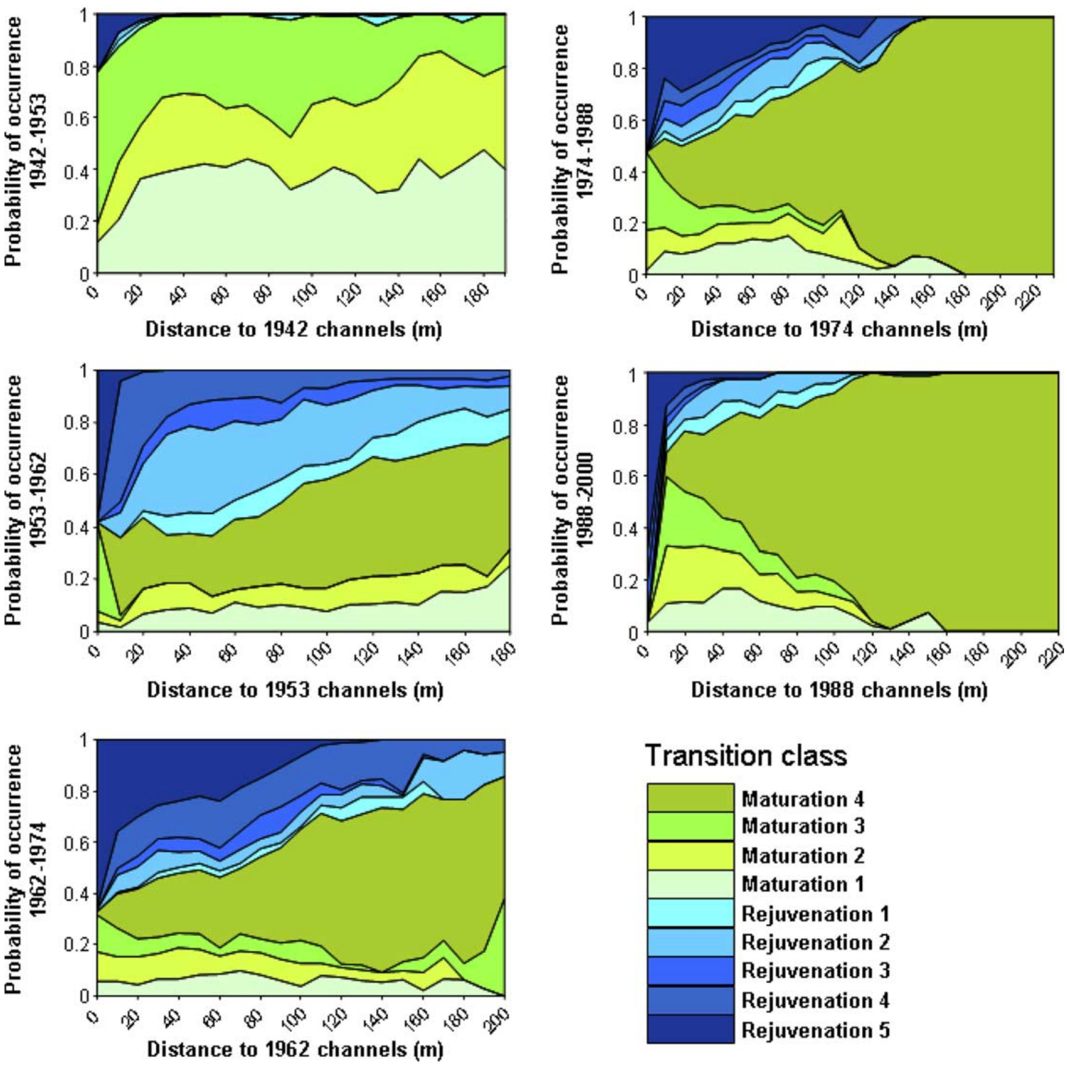

Figure 3. Probability of occurrence of the transition classes of maturation and rejuvenation at time t+1 (y axes) as a function of the distance to the active channels at time t (x axes). Blue colours correspond to transition classes of maturation and green colours correspond to transition classes of rejuvenation (transition classes are defined in Fig. 2).

(Steiger et al. 2001, Corenblit et al. 2007). However, the spatial pattern of stabilizing effects of vegetation, its lateral and longitudinal extension within the fluvial corridor and its duration, may vary according to contrasting bioclimatic, hydrogeomorphologic and anthropogenic contexts. The question if the results obtained on the River Tech could be transposed to other rivers remains at least partially unanswered, even though the biogeomorphologic succession may evolve in different settings according to a similar pattern or may be truncated. Wolman and Gerson (1978) suggested that within arid climatic river systems large floods can produce irreversible effects in the landscape structure because vegetation development is limited. Osterkamp and Costa (1987) demonstrated the aptitude of semi-arid rivers to rejuvenate regularly the biogeomorphologic succession at large scales within the fluvial corridors because vegetation concentrates only near the main channel. According to this landscape structure, Burkham (1972) and Schumm and Lichty (1963) observed respectively on the semi-arid River Gila, Arizona, USA and on the River Cimarron, New Mexico, USA, repetitive alternations between periods of concentration and important widening of the active channel. An equivalent landscape structure led on the River Tech to significant rejuvenations in the areas covered only by sparse vegetation during the 1960s and 1970s.

On the River Gila, Arizona, USA, the impacts of an exceptional flood still persisted in semi-arid landscapes after a period of fifty years (Burkham 1972, Tooth 2000). This slow evolution is in contrast with the River Tech for which a relaxation period following the destructive 1940 flood was estimated to be about thirty years. A general tendency to the decrease of the number of active channels was also observed within human impacted, regulated and channelized rivers (Eschner et al. 1983, Bravard 1989, Johnson 1994, Marston et al. 1995, Bravard et al. 1997, Shafroth et al. 2002). These dynamics were generally accompanied by the progression of riparian forests which contributed to reinforce the tendency toward channel incision and lateral biogeomorphologic stabilization. However, irreversible riparian forest dieback often occurred after few decades on regulated and channelized rivers due to important vertical channel incisions and to the absence of rejuvenation by lateral migration in the

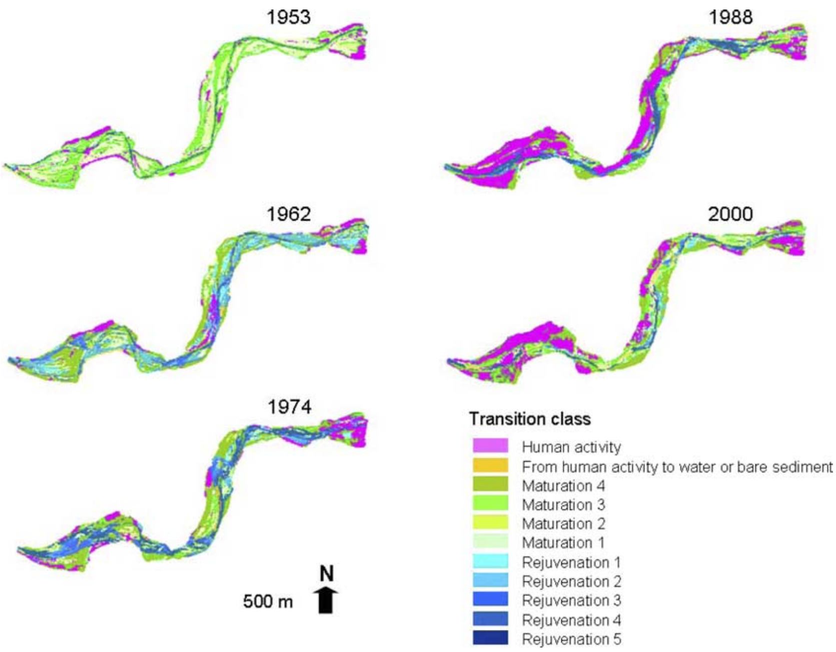

Figure 4. Maps of the studied river reach showing transition classes of maturation and rejuvenation including also areas with human activities and areas that shifted from human activities to open water or bare sediment. Map 1953 represents transitions between 1942 and 1953; map 1962 represents transitions between 1953 and 1962, and so far until map of 2000 which represents transitions between 1988 and 2000.

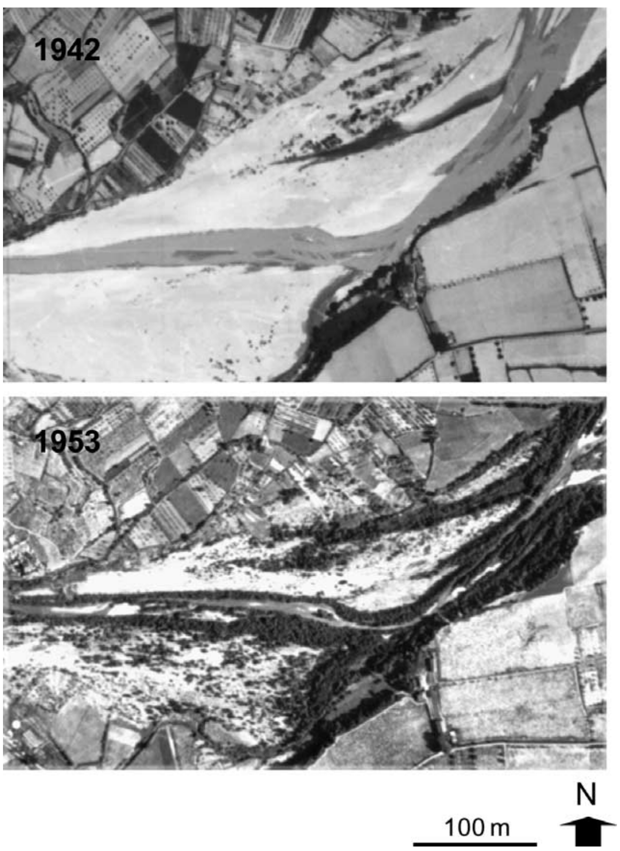

Figure 5. Aerial photographs illustrating the stimulation of vegetation succession along the active channels within the study reach between 1942 and 1953. This propensity was observed on aerial photographs for the entire River Tech corridor.

interval between very exceptional floods (Steiger et al. 1998).

The case of the River Tech which remains a relatively dynamic system in comparison to many other European rivers demonstrated that in the current Mediterranean bioclimatic context natural pioneer vegetation dynamics can be sufficient to produce a positive feedback leading to the expansion of riparian forests in the entire fluvial corridor and to floodplain construction. Thus, it is reasonable to argue that even moderate anthropogenic attenuation of flow variability and sediment transit strongly enhances this evolutionary trajectory in current Mediterranean bioclimatic conditions.

The mechanisms leading to the construction of islands and floodplains and the correlative expansion of post-pioneer riparian forests in thirty years can be explained on the River Tech according to local interactions between pioneer vegetation and hydrogeomorphology. The very good aptitudes of pioneer ligneous vegetation to regenerate quickly or to resist destruction by floods and to stabilize landforms (Francis et al. 2009) were attested by the empirical transition analysis (Supplementary material Table S1) and the Markov chain simulations (Fig. 7; Table 4). The biogeomorphologic phase, in particular when dominated by pioneer shrubs which intercept frequently water, sediment and diaspores (Gurnell and Petts 2006) was transitory and evolved rapidly and mainly toward the ecological phase (Fig. 3, 4 and 6; Supplementary material Table S1). The aptitude of pioneer ligneous vegetation to resist mechanical destruction during floods, to regenerate and to establish efficiently in disturbed areas was demonstrated by field studies for example on the Tagliamento River, Italy (Francis et al. 2005). *Populus nigra* and *Salix* spp. in particular have a very good fitness especially in response to intermediate hydrogeomorphologic disturbances (Karrenberg et al. 2002, Corenblit et al.

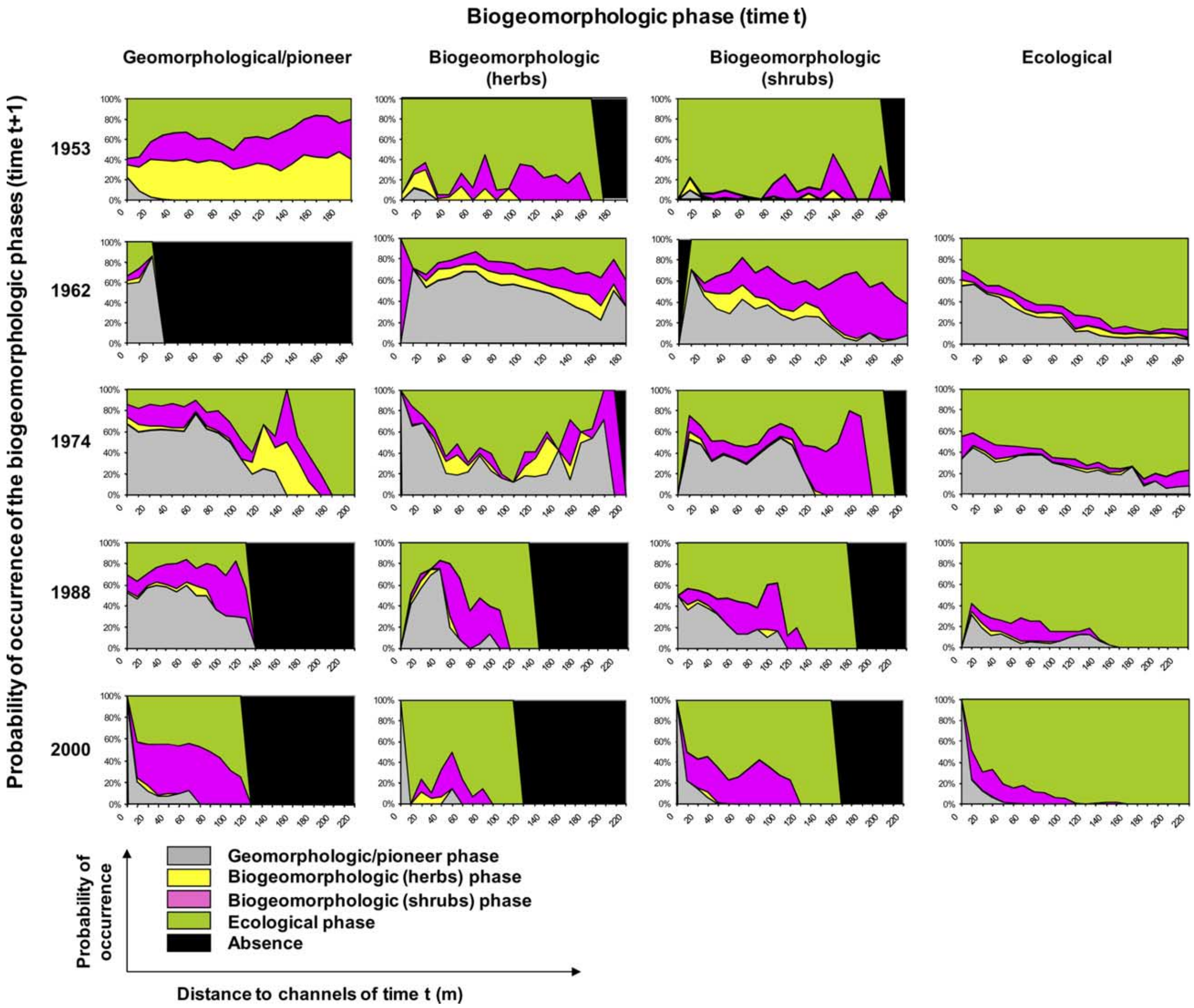

Figure 6. Probability of occurrence of the four different phases of the biogeomorphologic succession at time t+1 (e.g. 1953 corresponds to probabilities of occurrence between 1942 and 1953; 1962 corresponds to probabilities of occurrence between 1953 and 1962) (y axes) as a function of the distance to the active channels at time t (x axes).

2009a). Their life-history includes traits such as efficient dispersal, rapid germination, rapid root and aerial structure growth rates to withstand flooding and drought. Their ability to reproduce by vegetative processes was experimentally demonstrated on the Mediterranean River Drôme, France (Barsoum 2001) and on the River Tagliamento (Gurnell et al. 2005, Francis and Gurnell 2006). These different aptitudes control and largely increase the potential of stabilized and disconnected riparian forested islands and floodplains (Gurnell et al. 2001).

The implications of pioneer ligneous vegetation, in particular *Populus nigra*, *Salix* spp. and large woody debris able to resprout, in forming growing sediment accretion points are fundamental in temperate contexts in generating biogeomorphologic succession gradients (Pautou et al. 1997, Gurnell et al. 2005, Francis et al. 2009). Along the transverse gradient of hydrogeomorphologic disturbance, from the main active channels to the alluvial plain, pioneer meso-hydrophilous herbaceous vegetation and *Salix* spp. and *Populus nigra* developing in the exposed zones on alluvial bars demonstrated very strong resilience and physical resistance to mean-annual floods (T_{2-3} yr) during a complementary field study undertaken by Corenblit et al. (2009b) on the River Tech between 2002 and 2004. Discharges corresponding to the mean annual flood are assumed to be dominant for bedload transport in river channels, representing the theoretical optimum level for geomorphologic adjustment within channels and their immediate margins (Wolman and Miller 1960). Despite the erosion potential of the floods recorded between 2002 and 2004, pioneer vegetation stabilised the substrate, trapped large amounts of fine sediment and diaspores and progressed in succession near the active channels in a period of only three years (Corenblit et al. 2009b). The present study demonstrated in complement to the field observations that in such a biogeomorphologic context, and if no major destructive flood event occurs, fluvial landscape structure tends to be predisposed to evolve toward the domination by forested islands and floodplains at the scale of the fluvial corridor over thirty years. The main point to be made here is that such geomorphologic predisposition to riparian forest and floodplain resilience has a biological

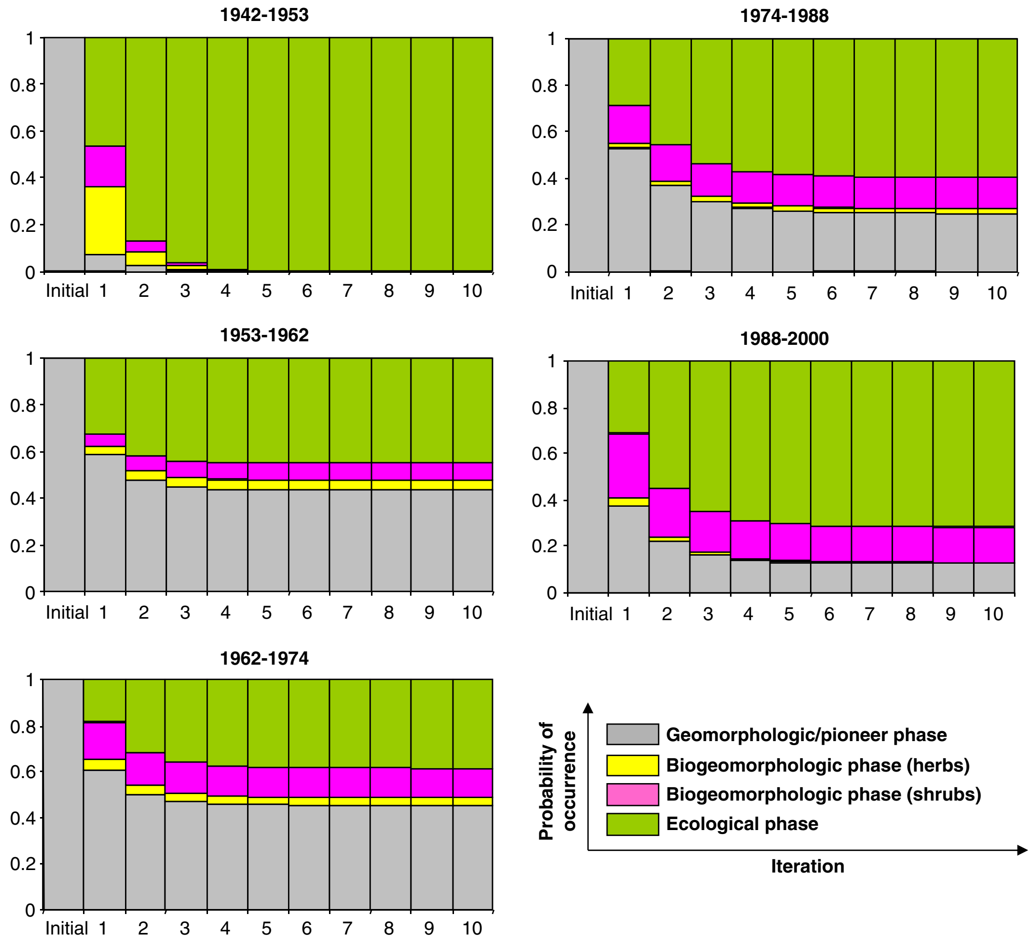

Figure 7. Markov chain analysis of the absorbent states over 1000 iterations corresponding to five approximately ten years periods between 1942 and 2000. Transition probabilities were calculated starting from the geomorphologic/pioneer phase.

origin linked to specific adaptations of pioneer riparian vegetation life-history traits, including morphological and biomechanical traits, in response to river disturbance regimes (Lytle and Poff 2004, Bornette et al. 2008, Corenblit et al. 2009a).

Equilibrium conditions of the biogeomorphologic succession

The analysis of biogeomorphologic succession rejuvenation versus maturation dynamics suggested that the evolution of

Table 4. Markov Chain analyses of transitions between phases of the biogeomorphologic succession. The simulations were undertaken over 1000 iterations. The mean return interval corresponds to the number of iterations before the return to the initial biogeomorphologic phase; the mean stability corresponds to the number of consecutive occurrences of a specific phase of the biogeomorphologic succession. Standard deviations are indicated for the mean return interval and the mean stability.

Phase	1942–1953	1953–1962	1962–1974	1974–1988	1988–2000
Relative frequency					
GEO/PION	0.00	0.48	0.45	0.23	0.11
BIOGEO_HERB	0.00	0.04	0.04	0.03	0.00
BIOGEO_SHRU	0.00	0.05	0.13	0.13	0.16
ECOL	0.99	0.43	0.38	0.61	0.73
Mean return interval					
GEO/PION	0.00 ± 0.00	2.47 ± 1.87	2.94 ± 2.31	6.63 ± 7.75	6.41 ± 5.53
BIOGEO_HERB	0.00 ± 0.00	20.20 ± 14.20	22.10 ± 22.70	43.7 ± 32.10	120 ± 187
BIOGEO_SHRU	0.00 ± 0.00	19.50 ± 19.20	6.72 ± 5.08	5.60 ± 5.46	5.60 ± 8.49
ECOL	1.00 ± 0.00	3.93 ± 3.71	4.26 ± 3.51	3.07 ± 2.61	2.6 ± 1.54
Mean stability					
GEO/PION	0.00 ± 0.00	3.11 ± 2.14	2.31 ± 2.10	2.08 ± 1.62	1.53 ± 0.66
BIOGEO_HERB	0.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00
BIOGEO_SHRU	0.00 ± 0.00	1.00 ± 0.00	1.09 ± 0.30	1.13 ± 0.35	1.28 ± 0.46
ECOL	Absorbing state	2.78 ± 1.92	2.40 ± 2.09	4.00 ± 3.08	4.35 ± 5.07

dynamic equilibrium (i.e. landscape structure displaying relatively stable characteristics with minor feedback mechanisms taking place, and to which it will return after disturbance) within the fluvial corridor is non-linear in time and non-homogenous in space at the scale of the reach scale as shown in Fig. 3 and Supplementary material Table S1. This observation can be associated mainly to 1) contrasting rates and patterns of vegetation establishment on the immediate margins and at long distances from active channels, and to 2) the consecutive reinforcement of the biogeomorphologic stability at the scale of the entire fluvial corridor over a thirty year period. The reinforcement of biogeomorphologic stability occurred when a threshold was reached. This threshold corresponded to the reinforcement of biogeomorphologic resistive forces after an initial state during which geomorphological remobilisation forces dominated. The occurrence of this threshold in time was largely controlled by vegetation dynamics, occurring when riparian forests became denser on the floodplain while pioneer vegetation establishment continued to be stimulated at the proximity of water channels on alluvial bars. Thus, a dynamic equilibrium for landscape structure resulting concurrently from maturation and rejuvenation processes was reached on the River Tech after thirty years following the catastrophic flood of October 1940. The spatial extension of rejuvenation and maturation reached respectively a total width of 30 and 200 m (i.e. 13% of the fluvial corridor dominated by rejuvenation and 87% by maturation processes) along the transverse gradient from the main channel to the floodplain. Comparable biogeomorphologic dynamics implicating *Populus nigra* and *Salix* spp. were also described on the Platte River, Nebraska, USA (Johnson 1994). These similar fluvial landscape trajectories on the River Tech and the Platte River attest an origin linked to specific effect and response traits of these engineering species (sensu Jones et al. 1994).

The transition analyses and Markov chain also suggested an increase in space and in time of the domination of biogeomorphologic resistive or cohesive forces over thirty years following a catastrophic flood in the Mediterranean context. In particular, as pointed out by Piégay (1997) on south-eastern French piedmont rivers, such increase of the overall biogeomorphologic stability over time can be attributed to the synergy between succession stimulation within the disturbed zone on well hydrologically connected alluvial bars and slow but progressive biogeomorphologic maturation on less exposed areas. The biogeomorphologic succession dynamics identified on the River Tech suggest the important implications of the dichotomy observed within the immediate margins of active channels with a rapid and intensive stimulation of pioneer vegetation establishment and a slow but constant development of riparian forests on floodplain areas less exposed to flood events. The last high magnitude floods ($T_{20–30}$ yr) observed on the River Tech since the 1980s did not produce significant rejuvenations of the biogeomorphologic succession which seems to have reached an attractor state corresponding to the domination by stabilized riparian forests. In a study undertaken in forested mountain river systems of the Pacific Northwest, USA, Beechie et al. (2006) identified a threshold for biogeomorphologic rejuvenation associated to migration of river channels occurring preferentially at a bankfull width of 15–20 m. Beechie and colleagues argued that larger channels are deep enough to erode below the rooting zone of banks densely colonised by vegetation. However, biogeomorphologic rejuvenation associated to lateral erosion and migration of the multiple channels with widths <20 m appears to be inhibited on the River Tech. Our results clearly suggest that the critical discharge needed to rejuvenate the biogeomorphologic succession at the corridor scale of the River Tech has to be larger than the one observed since 1988 with a recurrence interval $T_{20–30}$ yr. It seems likely that only exceptional events with a return period ≥ 100 yr, such as the 1940 flood, will be able to completely rejuvenate the biogeomorphologic succession on the River Tech.

Concluding remarks

The River Tech, a relatively natural Mediterranean fluvial system, was shaped by intermediate floods during the last sixty years which contributed to biogeomorphologic succession maturation. This river system demonstrated a high resilience over thirty years confirming, in the context of an intermediate disturbance regime in a Mediterranean setting, the hypothesis that such river systems tend to evolve mainly toward the ecological phase. These dynamics were initiated and reinforced by positive feedbacks of landform accretion and associated riparian vegetation succession. However, the evolution of the system from the geomorphologic toward the ecological phase and biogeomorphologic stability appeared to be non-linear with a threshold occurring thirty years after a major destructive flood. This threshold materialized a reinforcement of the biogeomorphologic cohesion at the scale of the corridor.

The associated effects of biogeomorphologic succession rejuvenation by floods in increasing biocomplexity and biodiversity are recognized (Baptist et al. 2004, Gurnell et al. 2005, Pettit and Naiman 2005) but are still difficult to evaluate. These effects on increasing landscape diversity were observed in this study on the River Tech during a period of thirty years following the flood of October 1940. Thus, restoring durably rejuvenation capacities for impacted rivers within the current anthropogenic and temperate bioclimatic settings appears today as a major but very complicated challenge. According to the results presented in this article, we suggest that progress in river restoration capacities will depend on our ability to achieve a better understanding of the reciprocal coupling between vegetation and hydrogeomorphologic dynamics and further quantifications of fluvial threshold dynamics in explicit relation with riparian vegetation effects and responses to hydrogeomorphologic disturbances in diverse bioclimatic and anthropogenic settings.

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